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EXPERIMENTS WITH TAPEWORMS.

I. SOME FACTORS PRODUCING EVAGINATION OF A CYSTICERCUS.¹

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During the past winter the opportunity came to me to try a series of experiments upon the bladderworm stage of *Tænia serrata*, one of the common dog tapeworms. The work was made easy because an abundance of material could be secured from the cottontail rabbit in this vicinity. As I have found no record of previous experiments of this kind, it has occurred to me that a brief account of them might be of general interest. One series of experiments in particular I shall here present for consideration. One of the methods used makes it possible to study the process of evagination in the living animal, and to readily secure evaginated cysticerci without the formality of passing them into the intestine of the host.

Tænia serrata is interesting historically from the fact that it was the species first used to demonstrate the characteristic life history of a cestode. Küchenmeister took the bladderworms, known as *Cysticercus pisiformis* Zeder, from the body cavity of hares and rabbits and fed them to dogs. In the course of two to three months he found they transformed and developed into the adult *Tænia serrata*, so that proglottides were detached and lost in the fæces. When the eggs of these forms were fed to hares or rabbits, after the second day of the experiment, minute whitish cysts were discovered in the liver tissue. Subsequently, in about thirty days these parasites left the liver and developed into the full grown *Cysticercus pisiformis*. It is to be noted that this life history involves a parasitism in two entirely different hosts. In general, in the first of these hosts the young tapeworm reaches a stage in development known as a cysticercus, and usually comes to rest in some particular tissue or part of the host's body. But in order to continue development it must be

¹ Contribution No. 5 from the Zoölogy Laboratory of the Kansas State Agricultural College.

transferred to the intestine of a second or definitive host. If this transfer is not made development stops, after a time death ensues, and degeneration of the young tapeworm takes place. However, if it reaches the intestine of the definitive host, barring accidents, it evaginates the already formed scolex, attaches itself to the mucous membrane by hooks or suckers, grows to maturity, reproduces hermaphroditically, and to complete the life history all that is needed is for the eggs to reach again the particular kind of individual that may serve as an intermediate host. This is of course a matter of common knowledge.

In order to fully understand the experiment it will be best to call to mind something of the structure of a cysticercus and the transformation which takes place when it reaches the intestine. Fig. 1 is a drawing made to show the general structure of a mature cysticercus taken from a half-grown wild rabbit. It is still enclosed within the cyst. When taken from the abdominal cavity a cysticercus consists of a whitish, elongated bladder-like structure filled with a watery fluid; at the smaller end is a dense, compact mass of tissue. Examination shows that this more solid portion of the bladderworm is due to an invagination of the anterior end as shown in Fig. 3. Within the cavity of the invagination is found the apparatus, the scolex, which serves for attachment to the walls of the intestine. In this case the scolex is provided with both hooks and suckers. A few hours after a cyst has been eaten by a dog, a young tapeworm, already transformed, may be taken from the intestine. In this process the invaginated portion evaginates, the scolex is everted, and the bladder digests or is separated and lost in the fæces. Fig. 2 is a drawing made from an evaginated cysticercus that was treated with artificial digestive juices, and Fig. 4 is an enlarged drawing of the scolex of the same.

Now if *Cysticercus pisiformis* is kept in physiological saline (0.7 per cent. NaCl) it never or rarely evaginates. Fifty-five specimens were left in such a solution for three days, in fact until many had died, and at the end of that time only five had evaginated. Besides this occasional evagination, one may produce eversion of the scolex by careful physical manipulation. Braun and Lühe state that this can be readily done in the case of

Cysticercus tenuicollis. "The parasite should be held just below the head-cone in the finger and thumb of one hand, while a regular pressure from within outwards is exerted with the fingers upon the head-cone. The head-cone will lengthen and if the manipulation is repeated several times, it will turn inside out and will hang down as a flat, wrinkled, contractile band upon the surface of the bladder. If pressure is now exerted upon the free end, the head will finally become everted, springing out with a sudden jerk." I have found the process of evagination is much more difficult to produce in the smaller *Cysticercus pisiformis*, and it is not believed that the contraction of stomach or intestine of the host could have any important rôle worthy of consideration in producing the eversion of the scolex.

We must therefore look upon the process of eversion as a response to chemical rather than to physical stimuli. For when fed to a dog practically all cysticerci may evaginate under favorable circumstances. In young, previously uninfected, dogs the percentage rose as high as 90 to 100 per cent. of infection. In old dogs the percentage of infection is not so high. Whether this is due to a sort of immunity dependent upon previous infection, or to some change in the strength of the digestive juices, I am unable to say.

Since it is highly improbable that physical stimuli have any important rôle in producing eversion, it was decided to try the plan of stimulating these animals with artificial digestive juices. The following formulæ were used as a basis in preparing the solutions used in these experiments:

1. For artificial gastric juice:

Water.....	100.0 parts	
Hydrochloric acid.....	0.2	" (dog, 0.3-0.5 part)
Pepsin.....	0.1	"

2. For artificial pancreatic juice:

Water.....	100.0 parts	
Sodium chloride.....	0.6	"
Sodium carbonate.....	0.2	" (dog 0.4 part)
Pancreatin.....	0.2	"

My solutions did not include all of the elements found in the natural product, but the calcium chloride and the potassium

phosphate are found in such small amounts in gastric juice that they were considered negligible. That they are not important factors in this experiment was verified by the results. For a similar reason diastase, potassium phosphate and lipase were not included in the artificial pancreatic juice which I used.

Two interesting questions had arisen in this connection: (1) Why is the young parasite not digested in the stomach? (2) What are the factors which influence or produce evagination? The answer to the first question is that as a matter of fact some of the cysticerci probably do meet the fate suggested, and that all react negatively to the gastric juice in such a way that its full effect is hindered or prevented. The answer to the second question will come out as we proceed.

In one of my experiments twenty cysticerci were removed from their cysts and ten were placed in each of two stender dishes. On these was poured a solution consisting of 0.4 per cent. of hydrochloric acid in which was dissolved a small amount of scale pepsin. Upon the addition of this liquid the bladderworms contracted strongly, especially at the invaginated end, and remained perfectly quiet, though they had previously been somewhat restless. The room temperature was about 90° Fahrenheit. Within an hour the bladders were digested enough so that they began to come apart. The cysticerci were left in this solution three and one half hours, and in all this time they showed no signs of activity, though the loose bladders were well digested. The acid solution was then removed and replaced by a solution containing the chief elements of artificial pancreatic juice as described above, leaving out the pancreatin. Within ten seconds several cysticerci had become active, and in a short time a few of them had evaginated. They were restless, however, and very soon all again drew in the scolex. Some pancreatin was now added to the solution; by the time this was dissolved most of the cysticerci were active and in the course of a few minutes ten out of twenty specimens had evaginated, though some of these had hardly completed the process. The dishes were then left over night. The next morning all were completely everted and most of them were relaxed in an excellent condition for preservation or study.

The preceding experiment indicates the probable grave danger that the parasite undergoes in passing through the dog's stomach. It also illustrates the quick response that the bladderworm gives to favorable or to unfavorable surroundings, and the response itself is a reaction to a chemical stimulus. After a considerable number of preliminary experiments in which the main facts of this paper were established, I planned a more complete series, one of which I shall give as typical of the entire set. The earlier experiments were conducted at room temperature.

First, I made up some solutions which contained the principal elements of gastric and pancreatic juices, the formulæ for which have been given. Second, several solutions were prepared containing different combinations of certain of these elements. In most cases the solution had as nearly as possible the same concentration of each component that is found in the natural digestive fluids of the dog. This is shown in the third column of Table I. Equal amounts of these solutions were next put in stender dishes and six well-developed and carefully selected cysticerci were placed in each solution. All stender dishes were then placed in a large water-bath in which the temperature varied less than one degree from $37\frac{1}{2}^{\circ}$ C. I was unable to examine this experiment until four hours and fifty minutes later, and this allowed more time than is ordinarily required for stomach digestion. The general results of this first examination are given in the fourth column of the table. It will be noticed that in lots 2, 3 and 10, in which hydrochloric acid alone was used, there was not a single case of evagination in the eighteen specimens. The same was true for lot 1 where sodium chloride was used. The best result was produced by the artificial pancreatic juice, lot 8, in which five out of six evaginated. The next best results were found in the enzyme solutions, lots 4, 7, and 11, though the reaction to the alkaline solution of sodium carbonate might be considered just as good, lot 6. The dishes were again examined the next morning, 21 hours after the beginning. This allowed considerably longer time than that required for complete digestion, and therefore the results shown in the last column do not come out in such contrast as they do when examined somewhat earlier. For subsequent work has shown that cysticerci

when about to die will sometimes evert the scolex under unfavorable conditions.

TABLE I.

TO SHOW THE RESULTS OF AN EXPERIMENT MADE TO DETERMINE THE EFFECTS OF CERTAIN SOLUTIONS UPON THE PROCESS OF EVAGINATION. ALL MATERIAL WAS KEPT IN A WATERBATH AT ABOUT $37\frac{1}{2}^{\circ}$ C. In lots 9, 10 and 11 the solutions were changed after four hours and fifty minutes.

Lot No.	No. Bladderworms Used.	Solution Used.	Result After 4 Hrs. 50 Min.	Result After 21 Hrs.
1	6	0.7% NaCl	None evaginated	1 evaginated
2	6	0.2% HCl	None evaginated	1 evaginated
3	6	0.4% HCl	None evaginated	1 evaginated
4	6	0.2% pepsin sol'n	1 evaginated	2 evaginated
5	6	H ₂ O—100 pts. HCl—0.4 pt. Pepsin—0.2 pt.	1 evaginated Bladders all digested	1 completely digested Bladder all digested
6	6	0.4 sod. Carb. sol'n	1 evaginated 1 almost evaginated	4 evaginated
7	6	H ₂ O—100 pts. 0.2% pancreatin	2 evaginated	4 evaginated (slightly acid)
8	6	H ₂ O—100 pts. NaCl—0.6 pt. Sod. carb.—0.4 pt. Pancreatin—0.2 pt.	5 evaginated	5 evaginated 1 not evaginated (young)
9	6	Sol'n lot 5 followed by Sol'n lot 6	0 evaginated	6 evaginated
10	6	Sol'n lot 3 followed by Sol'n lot 6	0 evaginated	5 evaginated 1 evaginated, partly
11	6	Sol'n lot 4 followed by Sol'n lot 7	2 evaginated	3 evaginated 1 partly evaginated

A study of the table shows the following special results: Lot 1 verifies previous observations, though the salt solution is here raised to body temperature. Therefore, we may conclude that temperature alone appears to have no important influence in producing evagination. From lots 2 and 3 it is also clear that hydrochloric acid interferes with or at least does not help eversion. The pepsin solution slightly aids the process as shown by a comparison of lots 4, 5, and 11. The pancreatin solution is a more favorable medium (lot 7). However, preceding a pancreatin solution by a pepsin solution does not seem to increase the

amount of evagination over that when it is used alone (lot 11). Lot 5 shows that artificial gastric juice is harmful to the cysticerchi for it tends to digest them and undoubtedly interferes with evagination (cf. also lot 9). This last effect is due to the acid. Artificial pancreatic juice as used in lot 8 is more effective than either of its elements used separately (cf. lots 1, 6, and 7). But we find that artificial pancreatic juice produces its best results when preceded by treatment with artificial gastric juice. In lot 9 this treatment gave 100 per cent. An almost equally good result was obtained in lot 10 when treatment with an acid (hydrochloric) was followed by an alkali (sodium carbonate).

This experiment or parts of it were repeated several times, but the results were invariably similar in character. Other experiments like these were tried upon the cysticerchi of *T. serialis*. The results were so much like those described that there is no need to give details here. The cysticerchi of this form are more apt to be digested by the gastric juice, probably due to their smaller size. While much remains to be done in this connection, it is believed that one may safely draw the following general conclusions:

1. Treatment with artificial gastric juice followed by immersion in artificial pancreatic juice furnishes a ready and efficient means of producing the evagination of cysticerchi of *T. serrata*. This is an easy method of obtaining material for preservation and for the study of the living parasites. It is best to use the gastric juice in a diluted form if one wishes to preserve the bladders intact.

2. In producing evagination the most important factors in artificial pancreatic juice are the alkali, sodium carbonate, and the extract of pancreatin. But to obtain the best reaction to these stimuli previous treatment with hydrochloric acid is required.

3. Treatment with an acid followed by an alkali (lot 10) gives rather better results than treatment with pepsin followed by pancreatin (lot 11). Hence the sodium carbonate appears to be a more important factor than pancreatin in producing evagination.

4. The cysticerchi are not digested in the stomach of the dog because they do not evaginate in a harmful acid medium. The

acid causes them to contract into as dense a mass as possible. This negative response to an inorganic acid is a fundamental and very general characteristic of protoplasm. For example, a very small amount of free acid produces fatal results upon protozoa, developing eggs, spermatozoa, and growing cells in general. "Sour" soils are unfavorable to the growth of most plants. Indeed, this experiment adds one more bit of evidence that one of the primary functions of the acid in the gastric juice is to kill bacteria and other living tissues that reach the stomach.

5. Finally these experiments suggest a way in which one may possibly determine why many tapeworms have a specific definitive host. Not that they have acquired a particular love for that host, but that the special host furnishes the right stimulus at the right time to call forth the proper reaction in the cysticercus. In another paper I have shown that these bladderworms will not produce tapeworms when fed to pigs, and there is one instance on record where a man swallowed five of them, without harmful results. We shall, no doubt, soon be able to explain much of this peculiar and specific behavior of parasites on the basis of a direct response to favorable or unfavorable physical or chemical stimuli. This will bring some of the little understood phenomena of parasitism into line with the brilliant work that has been done in recent years on the behavior of free-living forms.

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EXPLANATION OF PLATE I.

FIG. 1. Diagrammatic drawing of cysticercus of *T. serrata* enclosed in cyst. ($\times 4$.)

FIG. 2. An evaginated cysticercus of about the same size as the preceding. This specimen was treated with diluted artificial gastric juice followed by artificial pancreatic juice. ($\times 4$.)

FIG. 3. Optical section of the anterior end of the cysticercus shown in Fig. 1, with a rather complicated invagination. Drawn with aid of camera lucida. ($\times 18$.)

FIG. 4. Appearance of the scolex after evagination; parts slightly altered in position by pressure of cover-glass. Drawn with aid of camera lucida. ($\times 46$.)

